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Modelling water use efficiency in a dynamic environment: An example using *Arabidopsis thaliana*☆

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ABSTRACT

Intrinsic water use efficiency (W_i), the ratio of net CO_2 assimilation (A) over stomatal conductance to water vapour (g_s), is a complex trait used to assess plant performance. Improving W_i could lead in theory to higher productivity or reduced water usage by the plant, but the physiological traits for improvement and their combined effects on W_i have not been clearly identified. Under fluctuating light intensity, the temporal response of g_s is an order of magnitude slower than A, which results in rapid variations in W_i. Compared to traditional approaches, our new model scales stoma behaviour at the leaf level to predict g_s and A during a diurnal period, reproducing natural fluctuations of light intensity, in order to dissect W_i into traits of interest. The results confirmed the importance of stomatal density and photosynthetic capacity on W_i but also revealed the importance of incomplete stomatal closure under dark conditions as well as stomatal sensitivity to light intensity. The observed continuous decrease of A and g_s over the diurnal period was successfully described by negative feedback of the accumulation of photosynthetic products. Investigation into the impact of leaf anatomy on temporal responses of A, g_s and W_i revealed that a high density of stomata produces the most rapid response of g_s but may result in lower W_i.

1. Introduction

In order to meet the projected demand for cereal production by 2050, crop yields must improve by 1.16–1.31% each year; however, current estimates are well below this required rate [1]. The primary determinant of crop yield is the cumulative rate of photosynthesis over the growing season and is determined by the ability of the plant to capture light and CO_2, use this energy to convert the CO_2 to biomass, and how much of this biomass ends in usable yield. Improving photosynthetic efficiency is recognised as an important but unexploited avenue to increase yield potential in crop plants [2]. Increasing photosynthetic efficiency is accompanied by a higher CO_2 demand, which can be limited by the resistance of CO_2 diffusion into the leaf. Any attempt to decrease this resistance greatly increases the water loss by transpiration from the leaf.

Photosynthetic productivity is linked to water consumed by the plant and often measured as water use efficiency (*WUE*). *WUE* can be defined at different scales of time and space and, at the leaf level, it is often assessed as the ratio of CO_2 fixed per unit of H_2O transpired (E). Intrinsic water use efficiency (W_i) is defined when stomatal conductance to water vapour (g_s) is used instead of E. The use of g_s to describe the stomatal control on the rate of E facilitates the comparisons between different leaves and environmental conditions. The photosynthetic capacity of the leaf determines the net CO_2 assimilation (A) as a function of the variation in the microclimate surrounding the leaf. Over the diurnal period, A is mainly determined by the irradiance absorbed by the leaf and the limitation of CO_2 imposed by stomatal control. Under field conditions, environmental variables that affect both photosynthesis and stomatal behaviour are rarely constant. For example, light intensity (and spectral quality) alters in time scales of seconds to hours to which A and g_s must respond. The temporal response of A and g_s to a fluctuating environment are asynchronous, with g_s response often an order of magnitude slower than A, which results in rapid variations of W_i. Thus, it is important when describing the kinetic response of W_i to use an approach that considers responses by A and g_s simultaneously.

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Nomenclature

A	Net CO_2 assimilation
A_G	Gross CO_2 assimilation
R_d	Mitochondrial respiration
g_s	Stomatal conductance to water vapour
g_m	Mesophyll conductance to CO_2
g_b	Boundary layer conductance to water vapour
g_t	Total conductance to CO_2
W_i	Intrinsic water use efficiency
C_a	Atmospheric CO_2 concentration
C_i	CO_2 concentration in the intercellular airspaces
C_c	CO_2 concentration at the site of carboxylation
a	Stomatal pore area
a_s	Steady state target of stomatal pore area
a_{min}	Minimum stomatal pore area
a_{max}	Maximum stomatal pore area
α_L	Slope of the relationship
$\boldsymbol{\theta_L}$	Curvature factor of the curve
k_i	Time constant for an increase in a
k_d	Time constant for an decrease in a
L	Percentage of efficiency
SD	Stomatal density
D	Diffusivity of water in air
V	Molar volume of air
l	Depth of stomatal pore
P_a	The atmospheric pressure
S_a	Factor representing the influence of the rate of accumulation of sugars
S_e	Factor representing the influence of the rate of export of sugars
Vc_{max}	Maximum Rubisco activity
J_{max}	Maximum electron transport activity
α	Proportion of light absorbed by PSII

Intrinsic water use efficiency (W_i) is dependent on the anatomy (e.g. stomatal size and density) and the physiology (e.g. behaviour) of stomata as well as the leaf biochemistry (e.g. activity of the Calvin cycle), all of which interact to determine the kinetics of CO_2 and H_2O gaseous exchange between the leaf and atmosphere. The dynamic nature of the interactions between the different components that determine W_i are not fully understood and need to be addressed if we are to successfully improve both A and W_i under dynamic field conditions.

It is possible to conceptualise the inherent complexity of gas exchange over a fluctuating light regime through modelling, which will improve our understanding of the W_i response by simulating a number of gas exchange scenarios (e.g. changes in light intensity and humidity) that would normally be difficult to assess in a reasonable amount of time using experimental approaches. Current models focus on predicting g_s in steady state [3] and cannot be used to infer the impact of stomatal behaviour on A or W_i under dynamic conditions. Although temporal responses of g_s have previously been described using a dynamic model [4,5], the relationship between stomatal response and leaf level gas exchange was not clearly described. We propose to use a model that will take into consideration the anatomy and physiology of stomata to more accurately represent the stomatal control of W_i.

To scale stomatal responses to leaf level g_s, the two most important stomatal characteristics are aperture and density [6–8]. A high stomatal density does not necessarily result in a higher g_s as stomata ultimately control their aperture depending on the guard cell responses to the external (e.g. light intensity) and internal (e.g. mesophyll demand for CO_2) stimuli [9]. To link stomatal behaviour to leaf level gas exchange responses, we propose a ‘big stoma’ approach that consists of simulating the response of one stoma that is representative of the heterogeneous response of many stomata and scaling the response to the leaf level. This approach was incorporated in an enhanced version of the multi compartments model described by Noe and Giersch [10] to predict A and W_i. Scaling up the dynamic of the stomatal response to the leaf level, with the improved model for CO_2 diffusion inside the leaf, will help to dissect W_i into traits of interest and predict potential gains in W_i.

The objective of this study was to develop a new model combining our most recent knowledge of kinetics in stomatal behaviour and photosynthesis to describe the temporal response of W_i over the course of a day with natural dynamic variations in irradiance. All the parameters of the model described here incorporate a trait of interest for W_i and were adjusted using Bayesian inference. The model was validated using a dataset with a different irradiance pattern to assess the predictive power of the model. A sensitivity analysis was finally performed to show the interaction among the parameters and display the potential gain in W_i in the case of one or two parameters changing. We used the output of the model to understand how temporal responses in g_s impacts A and W_i.

2. Material and methods

2.1. Dynamic modelling of photosynthesis and stomatal conductance

The model essentially consists of four differential equations describing the diffusion of CO_2 between different compartments represented by the atmosphere, the intercellular air spaces and the photosynthetic tissues (Fig. 1). The exchanges between these compartments are dependent on the stomatal aperture and the resistance of diffusion in the mesophyll cells. In addition, the model took into account the limitation of photosynthesis and stomatal aperture that appeared during a period of light.

$$\begin{cases} \dfrac{da}{dt} = \dfrac{a_s - a}{k_i} if a < a_s \\ \dfrac{da}{dt} = \dfrac{a_s - a}{k_d} if a \geq a_s \end{cases} \tag{1}$$

The first differential equation (Eq. (1)) described the temporal variations of the stomatal pore area (a) with a_s the steady state target followed by a and two time constants, k_i and k_d, for an increase or a decrease of a respectively. Considering the spatial heterogeneity of the stomatal response, a top-down approach was used, signifying that the model simulated the response of one stoma representative of the sum of the individual stomatal responses and scaled it to leaf level instead of trying to integrate the response of each stoma.

The steady state target of a (a_s) as a function of the light intensity (PPFD) was predicted using a non-rectangular hyperbola [4]:

$$a_s = \left[a_{min} + \frac{\alpha_L PPFD + (a_{max} - a_{min}) - \sqrt{\alpha_L PPFD + (a_{max} - a_{min})^2 - 4\theta_L \alpha_L PPFD(a_{max} - a_{min})}}{2\theta_L}\right] \cdot L \tag{2}$$

with a_{min} and a_{max} the minimum and maximum stomatal pore area, α_L the slope of the relationship, θ_L the curvature factor of the curve and L the percentage of efficiency (see below).

$$\frac{dC_i}{dt} = \left[g_t\left(C_a - C_i\right) - g_m\left(C_i - C_c\right)\right]\frac{RT_l}{d_a P_a} \tag{3}$$

Eq. (3) described the variation of the CO_2 concentration in the intercellular airspaces (C_i) with C_a the atmospheric CO_2 concentration and C_c the CO_2 concentration at the sites of carboxylation.